On the Cœlom, Genital Ducts, and Nephridia.

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With Plates 44 and 45.

The chief object of this paper is to call attention to a theory of the homology of the cœlom which has been gradually gaining ground abroad, but has not, I venture to think, received in this country the notice which it deserves. The theory I refer to is, that the cavity which we know as the cœlom in the higher Cœlomata is represented by that of the genital follicles in the lower types of that grade. Ever since Hatschek wrote the often-quoted words: "Die secundäre Leibeshöhle verhält sich wie die Höhle der Geschlechtsdrüse der niedrigeren Formen," and pointed out that true mesoblastic metamerism is really due to the repetition of the gonads (**48**), so many favourable new facts have been brought to light, that from a suggestion the statement has become a well-established theory. In a most interesting and suggestive paper on the ancestry of the Annelids, Dr. E. Meyer has set forth the theory in some detail (**81**). After showing that the cœlomic cavities in the Polychætes are quite comparable in development and function with the genital follicles of the Planarians, he further maintains that the theory throws a flood of light on various otherwise obscure questions, such as the bilateral character of the cœlom, its invariable connection with the genital cells, the absence of a truly unpaired prosto-

mial cœlom, &c. He then treats of the nephridia and genital ducts, and it is with this part of the question that I wish more especially to deal in this paper. Meyer holds that the nephridium of the Platyhelminths is represented by the so-called head-kidney in the first segment, and by the tube of the nephridium in the trunk segments of the Annelids, while the genital duct of the Platyhelminths is represented by the wide funnel of the trunk nephridium which develops, independently of the tube from each genital or cœlomic follicle, and becomes grafted on to it afterwards. Unfortunately, the author restricts his remarks almost entirely to the Polychætes and those forms which appear directly to lead up to them. Although the theory has been at all events partially adopted by other writers (Lang, **71**; Korshelt and Heider, **67**), no one, as far as I am aware, has pushed it to its logical conclusion, and applied it to all the groups of Cœlomata. This is what I shall attempt to do in this paper. First of all, however, there is one thing to be noticed with regard to Meyer's general statement about the nephridial funnel, namely, that since the publication of his own researches on the Polychæta, and of those of Vejdovsky and others on the Oligochæta, there can be no doubt that the nephridial funnel in the latter forms part of the true nephridium (is, in fact, derived from the end-cell), and is not a grafted genital duct, as is the case in some at least of the Polychæta.

An unprejudiced review of the well-established and recently ascertained facts concerning the development of the excretory organs and genital ducts of the Cœlomata must, I think, inevitably lead us to the conclusion that we have been confusing two organs of totally different origin under the one name nephridium—the one organ the true nephridium, the other the morphological representative of the genital duct, which may be called the peritoneal funnel, to avoid confusion. Further, that while on the one hand in certain groups such as the Planaria, Nemertina, Hirudinea, Chætopoda, Rotifera, Entoprocta, besides the genital ducts or peritoneal funnels, we find true nephridia in the adult; on the other hand, in such

groups as the Mollusca, Arthropoda, Ectoprocta, Echinoderma, and Vertebrata, there are in the adult no certain traces of true nephridia. In these latter groups, as we shall see, the peritoneal funnels (primitive genital ducts) take on the excretory functions of the nephridia which they supersede.

In the following brief review of the various classes of Cœlomata, I shall endeavour to show that the two kinds of organs can always be distinguished; that the first, the nephridium, is primitively excretory in function, is developed centripetally as it were, and quite independently of the cœlom (indeed, is probably derived from the epiblast), possesses a lumen which is developed as the hollowing out of the nephridial cells, and is generally of an intracellular character, is closed within, and may secondarily acquire an internal opening either into a blood space or into the cœlom (true nephridial funnel as opposed to the peritoneal funnel); and that the second kind of organ, the peritoneal funnel, is primitively the outlet for the genital products, is invariably developed centrifugally as an outgrowth from the cœlomic epithelium or wall of the genital follicle, is therefore of undoubtedly mesoblastic origin, and possesses a lumen arising as an extension of the cœlom itself.

In the series of diagrams illustrating this paper, based on the most recent and accurate researches, it has been my constant endeavour to interpret the author's results correctly, and not to distort the facts in favour of the theory here advocated.

Planarians.

The nephridia of the Planarians, as is well known, are formed of a main duct, which branches out into fine tubules ending blindly internally in flame-cells (fig. 1); they do not develop beyond this "pronephridial" condition—protonephridium of Hatschek (55). The arrangement of this single pair of nephridia is extremely variable; the two organs may join and open by a median external pore near the mouth or behind, or they may open by a number of pores at the sides. Gunda segmentata, a most interesting form described by Professor Lang (69), possesses longitudinal main trunks into which

open the fine branches ending in flame cells, and from which pass segmental ducts to the exterior, corresponding to the segmentally arranged gonads. It is by the breaking up of such a system into separate organs that Lang would derive the nephridia of the higher Cœlomata.

Unfortunately, we know little about the origin of the nephridia in this group. Lang has described, in Discocelis, paired ingrowths of the epiblast, which he believes give rise to the nephridia (**70**). This observation strongly supports his theory as to the phylogenetic derivation of the nephridia from epidermal glands; and, indeed, it seems pretty certain that an incipient excretory organ to be efficient must have been derived from, or at all events situated close to, the surface layer in order to get rid of its excretory products.

It is in the Planarians, a group undoubtedly primitive[1] in some respects, that we should expect to discover the cœlom in its first stages of development, and, in fact, we do seem to be able to trace it from its first appearance. In some Acœla (Graff, **42**, **44**), and other simple forms, the gonads consist merely of the genital cells lying freely in the parenchyma. In others, these cells become surrounded by an epithelium formed by the adjacent cells; the epithelial sacs, one on either side of the body, may then become hollow, while the wall grows out to form two tubes, the genital ducts (peritoneal funnels). Another important stage is presented by these organs in Gunda segmentata (Lang, **69**). Here the genital follicles are repeated segmentally, the first pair being ovarian, the rest testicular sacs. If these

[1] One of the most useful lessons of modern research has been to teach us with what great care the word "primitive" should be applied to any group of existing animals. A few years ago naturalists readily derived one group of living animals directly from another, apparently more primitive; but their genealogical trees are now becoming reduced to bushes, in which the branches spring from a common base. Nevertheless, it is true that certain groups may retain, either in their general organisation or in some particular details, characteristics of the ancestors from which they have diverged. The Planarians, with their complicated nephridial and genital apparatus, their deeply-sunk nervous system, yet generally archaic plan of structure, are a striking case in point.

follicles were larger, Gunda segmentata could be called a truly segmented animal.[1] The inner ends of the genital ducts are formed as outgrowths from the genital follicles: "Der Oviduct ist bei Gunda segmentata, wie bei Planaria torva anfangs ein solider Zellenstrang. Zweifellos ensteht er durch Wucherung aus dem soliden ovarium selbst, ähnlich wie die Samenleiter Auswüchse der Hoden sind" (observations confirmed in his later work, 70).[2] The oviduct becomes hollow and ciliated, and grows backwards to the genital pore; the vasa efferentia fuse to form the main sperm-duct.

To sum up, then. In the Planarians the excretory organs are a pair of pronephridia, probably derived from the epiblast; the gonads arise from a mass of cells in the mesoblast, which may become hollowed out into a genital follicle (cœlomic sac) from the wall of which arise the genital cells. The follicle grows out to form the genital duct (peritoneal funnel), which joins an epiblastic invagination at the genital pore (fig. 1).[3]

[1] E. Meyer believes (81) that the ancestor of the Annelids possessed a pair of long genital follicles, and that metamerism was brought about by their being broken up at intervals, chiefly to facilitate its serpentine motion; each portion would then have acquired its own duct to the exterior. It seems to me more probable that the metameric arrangement of the genital follicles is more directly due to that "tendency" to repetition by a sort of budding, which is seen in the case of the gonads, the penes (Anonymus), and even the pharynx (Phagocata; Woodworth, 112) amongst the Planarians, and again, perhaps amongst the Mollusca (for a full discussion see Bateson, 3).

[2] Jijima's account of the development of the sperm-ducts differs somewhat from that of Lang, but he derives both from the mesoderm (60).

[3] The spaces contained in the connective tissue or parenchyma have been sometimes compared with the cœlom; these spaces seem rather to represent the vascular system of the higher Cœlomata. I need not treat here of the homology of the vascular system, which is probably of quite separate origin from the cœlom. Professor Ray Lankester's view, that the blood-system is simply a liquefaction, as it were, of the mesoblast, seems to me to agree perfectly with the facts. Moreover, the theory held by many authors that it is directly derived from the blastocœl appears to be quite untenable. As Professor Lankester has pointed out to me, if this were the case we should expect to find the blood-spaces best developed amongst the Diploblastica; now it is just in the (adult) Cœlenterates that it is entirely absent. Indeed we may say that the blood-space, or hæmocœl, does not appear in phylogeny

About the Cestodes and Trematodes it need only be said that they are built (so far as concerns the question discussed in this paper) upon essentially the same plan as the Planarians;[1] while as to the Nematodes, of the development of which we know too little, it seems probable that here also the genital follicles represent the cœlom, while the body cavity is a blood-space corresponding in its relations to the parenchyma of the Planarians.

Rotifera.

The Rotifers, recently described in great detail by Platte (**87, 88**) and Zelinka (**115**), agree in the general structure of the nephridia, genital follicles, and genital ducts, so closely with the Platyhelminths that they may be dismissed with a very few words. The nephridia are a pair of branching tubes ending internally in flame cells, and opening behind into the cloaca.[2] The cœlom is represented by a pair of genital follicles, one of which only is generally developed; the wall of the follicle is produced backwards to form the genital duct, or peritoneal funnel opening into the cloaca.

The development of the nephridia has not yet been thoroughly worked out. Zelinka has traced them to a group of cells of doubtful origin. He adds: "das Exkretionssystem konnte ich in so fern mit Sicherheit auf das Ektoderm zurückführen, als es bestimmt nicht auf das Entoderm bezogen werden kann" (**115**).

until the mesoblast has been formed, and, generally speaking, that the greater the development of mesoblast the more definite is the vascular system. I should rather consider the connection of the blood-spaces with the blastocœl as arising for purely mechanical reasons, so to speak, and in no way of phylogenetic significance. The temporary continuity of the blastocœl with the blood-space during the ontogeny of certain of the higher forms would seem to be connected with that method of development by the folding of germ-layers or sheets of tissue, which no one would look upon as primitive. During this process, the cavities which will form the vascular system later on, are inevitably continuous with the space left between the germ-layers.

[1] Fraipont maintains that the flame end-cells of the nephridia of the Cestodes and Trematodes communicate internally by means of a small lateral aperture (**39**).

[2] As in the case of some Platyhelminths, the nephridia have been stated to open internally (Eckstein, **28**).

Entoprocta.

This group also, from our present point of view, differs little in its organisation from the Planarians.

A pair of nephridia—short tubes, generally with an intracellular lumen and ending in a flame-cell or a group of cells with cilia,—open by a median pore in front of the genital pore (fig. 4) (Hatschek, **47**; Harmer, **46a**; Ehlers, **29**; Davenport, **26**). Possibly in some forms they open internally (Joliet, **61**), and in Urnatella they may be connected with a system of branching tubules ending in flame-cells (Davonport, **26**). The origin of the nephridia is doubtful; Hatschek traced them in the embryo to cells which he believed to be mesoblastic (**47**).

Embedded in parenchymatous tissue are a pair of genital follicles (fig. 4). From each a typical peritoneal funnel leads to a median pore (Ehlers, **29**).

Mollusca.

We now have to deal with a group of animals in which, as I shall endeavour to show, the embryo is provided with a pair of true nephridia; later, when the two cœlomic sacs belonging to the unsegmented trunk have acquired a considerable size, the peritoneal funnels formed from their walls take on the excretory function, whilst the nephridia degenerate [1].

True nephridia have been described in all the groups of Mollusca except the Isopleura and the Cephalopoda, and have recently been the subject of a special study from Dr. R. von Erlanger (**34**, **35**). They consist of short tubules formed, as a rule, of one or of a small number of cells, pierced by a canal which communicates with the exterior by a pore behind the velum (fig. 20). The inner end of the nephridium is provided with a flame-like bunch of cilia, or with a flagellum. An internal opening into the blood-space or head-cavity has been observed in some forms, such as Lymnæus, Helix (de Meuron, **79**; Jourdain, **62**; Fol, **38**; Sarasin, **92**; Wolfson, **111**; v. Erlanger, **35**, &c.), Teredo (Hatschek, **50**), and perhaps in

[1] This view evidently obviates the difficulty some have felt as to the presence of two pairs of so-called nephridia in an animal composed of one segment.

Cyclas (Ziegler, **116**). In other cases, such as Paludina, and Bythinia (v. Erlanger, **32**, **33**), the nephridium appears not to open internally, but to remain in the pronephridial stage.

The first stages in the development of the nephridium of the Mollusca have, unfortunately, not yet been satisfactorily worked out. Rabl (**88a**) derives the nephridium in Planorbis from a large cell which also gives rise to the mesoblast. Wolfson traced that of Lymnæus, which, he says, is derived from a large in-wandering epiblastic velar cell on either side (**111**). Hatschek (**50**), v. Erlanger (**32**, **33**), and others trace it to cells which they consider to be of mesodermal character, but the exact origin of which is not clear.[1] In some cases a late epidermal invagination is said to take place at the nephridiopore which forms the peripheral end of the duct (v. Erlanger, **32**, **34**).

We must now examine the development of the excretory organs of the adult Mollusca, which appear to be nothing but peritoneal funnels. An accurate description of the development of Paludina has recently been given by R. von Erlanger, and although the ontogeny is much modified owing to the asymmetry of the adult, I shall begin with it as it is the only detailed account we have. The genital follicles or cœlomic sacs (pericardium) arise as a cavity on either side, a hollowing out of the mesoblast (fig. 20). These cavities enlarge and fuse below the gut. On either side a thickening takes place on the ventral wall of the cœlom, which here grows out in the form of a typical peritoneal funnel (fig. 21). The right peritoneal funnel then enlarges and fuses with an epidermal invagination, which forms the outer end of the excretory organ. "Was die Niere anbelangt," says von Erlanger, "so bin ich der Ansicht, dass der secernirende Abschnitt derselben aus dem Mesoderm

[1] I think we may safely say that there is nothing which precludes the possibility of the nephridia being primitively derived from the epiblast, as they appear to be in the Platyhelminths, Rotifers, and Chætopods; although the fore-easts may sink in at a very early stage and thus become included in that "Anlagecomplex" which we eall mesoblast. In Helix, de Meuron derives them from the epiblast, but he is not positive about the internal extremity (**79**).

stammt und dass diejenigen Beobachter, welche ihr aus dem Ektoderm enstehen lassen, entweder nur den ausführenden Theil der Niere berücksichtigt haben oder, was noch häufiger geschicht, die beiden Abschnitte nicht in ihren Zusammenhaug erkannten: Der ausführende Theil wird nämlich von Allen, mit Ausnahme von Rabl, aus einem Theil der Mantelhöhle abgeleitet" (32). On the left side, to which the genital function is restricted, the gonad develops from the wall of the cœlom; then, together with the rudimentary left peritoneal funnel, it becomes constricted off from the main division of the cœlom (the pericardium), forming a small genital sac. From the wall of this sac the genital duct grows out, and joins an epidermal invagination, like the peritoneal funnel of the right side. Doubtless the genital duct is really the left peritoneal funnel, as v. Erlanger suggests: "Ich konnte . . . . feststellen, dass die Anlage der Genitaldrüse in der ursprüngliche linken Hälfte des Perikards ensteht, und zwar ungefähr da, wo sich die rudimentäre linke Niere zurückgebildet hat. Eben so ensteht auch die Anlage des Ausführganges an der Stelle, wo der rudimentäre Ausführgang der linken Niere sich befand, und scheint einfach aus diesem hervorzugehen." These observations have been fully confirmed in the case of Bythinia (33), and the conclusions, as we shall see shortly, are supported by the comparative anatomy of the Mollusca in general (fig. 22).

Ziegler has described the development of Cyclas cornea, which in some respects is less modified, the adult being symmetrical (116). Here also the cœlom (pericardium) arises as a right and left follicle. The two cavities enlarge, surround and fuse below the gut. On either side the organ of Bojanus develops as a peritoneal funnel, which meets an epidermal invagination (fig. 22).

In the Mollusca, then, we find at an early stage a pair of true nephridia (Urniere, head-kidneys), possibly of epiblastic origin. The cœlom develops as two cavities in the mesoblast, genital follicles, from the walls of which grow out two peritoneal funnels, the organs of excretion and carriers of the

genital cells of the adult. It can hardly be doubted that primitively the renal organs (organs of Bojanus, nephridia of authors) functioned as genital ducts. Such is, indeed, still the case in Chætoderma, the Neomenians, and the Zygobranchia. Also in the most primitive Lamellibranchs, such as Nucula and Solenomya, the peritoneal funnels still retain their original function. As Pelseneer has shown (86), gradually a separate genital duct has been split off, which in Anodon, Cardium, &c., opens independently. Intermediate stages are found in such forms as Pecten, and Spondylus, where the genital cells are shed into the kidney itself; and in Arca, Ostrea, &c., where the kidney and genital duct open into a common cloaca. Likewise in the Chitons a separation has taken place of the genital region of the cœlom from the renal; the gonad then acquires special ducts, which may not be homologous with peritoneal funnels. In the Cephalopoda, although the cœlom remains continuous, special apertures serve for the escape of the genital cells; whether these should be considered as a second pair of peritoneal funnels is also doubtful.[1]

(The aberrant form Rhodope veranii would appear to be amongst the Mollusca, if it be really of that class, the only one which retains true nephridia in the adult. It is provided with a pair of branching tubes, opening by a common pore, and ending internally in flame-cells. The cœlomic or genital follicles, ovarian and testicular, are small and numerous. Their ducts join to a common hermaphrodite duct, which again divides into two openings by male and female pores [43, 12].)

Dinophilus.

For our purpose it will be convenient to treat this genus separately, and not with the Archiannelida which will be included with the Polychæta. It is of great interest, since, in some species at least, the nephridia are metamerically repeated whilst the cœlom is represented by a single pair of genital follicles.

[1] Such a case may be compared to that of certain Nemertines, where numerous genital follicles and as many genital ducts are present in one segment, and to the similar arrangement in the Vertebrates.

In Dinophilus apatris, Korschelt has described flame-cells which he believed to be connected with a longitudinal canal opening posteriorly (66). E. Meyer, however, has figured in D. gyrociliatus five pairs of typical closed nephridia, or pronephridia, ending in flame-cells internally, and disposed metamerically according to the outer signs of segmentation (80). Harmer (46) describes five pairs of very similar nephridia in the female D. tæniatus. In the male there are four pairs of nephridia, perhaps with internal openings.[1]

The testes are a large right and left sac, which fuse across the median line; as Harmer himself says, it is "possible that in the connective-tissue lacunæ of the body of Dinophilus we have the representative of the so-called 'primary body-cavity,' whilst in the fully developed male the 'secondary body-cavity' is represented by the cavity of the testis, with which the funnels of the vesiculæ seminales are connected." It might be added that these funnels, which form the inner openings of the sperm-ducts, have all the appearance of true peritoneal funnels, comparable to the genital ducts of the Platyhelminths, and the other groups already spoken of.

The paired ovarian cavities appear to be provided with only very degenerate ducts, reduced to mere pores in D. vorticoides and D. apatris (compare the Archiannelida and the female ducts of certain Oligochæta such as the Enchytrœids).

The structure of Dinophilus might be explained in one of two ways. Either it has acquired a number of nephridia, whilst retaining the primitive single pair of genital follicles; or it is a degenerate form which has lost its metamerically repeated genital follicles, whilst retaining a number of separate nephridia. Our present knowledge does not enable us to conclude for certain which of these explanations is the correct one.[2]

Histriodrilus Benedeni (Histriobdella homari) may

[1] The fifth pair is possibly, according to Harmer, represented by the distal portion of the genital ducts leading to the penis (compare with certain Polychæta where the nephridium fuses with the peritoneal funnel).

[2] In a paper which has just appeared Schimkewitsch describes a ladder-like nervous system, and traces of segmentation in the developing mesoblast ('Zeit. f. w. Zool.,' Bd. lix, 1895).

be closely related to Dinophilus. It possesses five pairs of pronephridia (four in the female), and a distinct cœlomic or genital cavity also opening by one pair only of peritoneal funnels to the exterior (Foettinger, **37**). Here it seems to be pretty certain that there was originally a segmented cœlom; there is still a ventral chain of ganglia.

Nemertina.

The nephridia of the Nemertines consist essentially of a longitudinal canal on either side of the anterior region of the alimentary canal, opening to the exterior by one or by several pores situated laterally at more or less regular intervals (von Kennel, **63**; Oudemans, **85**; Hubrecht, **59**; Burger, **15**, **17**). Internally they have been stated to open into the blood-vascular system; the latest researches, however, do not support this view (**15**), and Bürger has shown that in several species the nephridial canals give off fine branches ending in bunches of flame-cells (**17**) (figs. 2, 3, and 24; in these diagrams the nephridia are represented in the same region as the gonads).

Although the development of the nephridia has not been followed out in detail, Hubrecht (**58**) and Bürger (**18**) have traced their origin from direct invaginations of the epiblast.

In this group of elongated worms the genital follicles are numerous, and generally arranged in pairs, alternating with the intestinal cæca. Each follicle communicates with the exterior by a duct or peritoneal funnel, formed as an outgrowth from its wall at a comparatively late period (figs. 2, 3, and 24). It is hardly necessary to emphasise the striking similarity between this metameric arrangement of follicles with their corresponding ducts and the almost identical metameric cœlomic follicles and genital ducts of the Chætopods.[1]

Oligochæta.

Thanks to the numerous researches of Profs. Hatschek,

[1] R. S. Bergh, in 1885, in a paper which I have not seen, pointed out the resemblance between the genital follicles of the Nemertines and the cœlomic cavities of the Chætopods; but he considered the ducts of the follicles to be homologous with the nephridia of the latter group (**6**).

Bergh, Wilson, Vejdovsky, and others, we have now a very detailed history of the development of the nephridia in the Oligochætes.

The observations of Hatschek, Wilson, and Bergh do not coincide in many particulars; but all these discrepancies have been so admirably reconciled by Vejdovsky in his careful work on Rhynchelmis and other forms (**101**), that we can, I think, be now quite confident that we have a satisfactory account of the embryology of these organs; more especially since these results have been in many respects amply confirmed by the researches of Whitman, Bergh, and Bürger on the Hirudinea.

The development of the nephridium in Rhynchelmis has been most carefully described by Vejdovsky (**101**). In the first stage he figures it consists of a large cell (trichterzelle or funnel-cell) within or on the posterior surface of the septum. This "funnel-cell" divides and gives off a string of small cells behind, from which is developed the canal of the nephridium. A large vacuole appears between the two cells formed from the funnel-cell itself, in which a flame-like flagellum is developed. Vacuoles now arise in the posterior string of cells, fuse together, and form the lumen of the canal which communicates with the end-chamber containing the "flame" (figs. 6 and 25). Finally this chamber opens into the cœlom, and the posterior loop joins the skin; a communication is established with the exterior by means of a secondary invagination of the epidermis—the end-vesicle. Quite similar is the development of the nephridium in Stylaster and Tubifex (Vejdovsky, **100**).

Bergh (**9** and **10**) traced back the nephridia in Criodrilus and Lumbricus to a large cell, the funnel-cell, lying close to the epiblast and between each successive pair of solid mesoblastic somites. When these become hollowed out, the funnel-cell buds off posteriorly a chain of cells, the future canal of the nephridium; vacuoles appear in these cells, as in Rhynchelmis, to form the lumen. Meanwhile the funnel-cell itself, which has retained its large size, pushes through the mesoblast to reach the cœlomic cavity in the segment in front; here it divides, acquires cilia, and becomes the funnel of the adult nephridium.

The posterior canal grows to the surface, where it opens through the epidermis; in some cases there is here an invagination of the epidermis to form the end-vesicle (Vejdovsky).

As to the origin of the funnel-cell—the forecast of the whole true nephridium: it arises from the primitive cell row, or nephric cord, formed by the repeated division of one of the teloblasts on either side. In the earlier stages this teloblast and the nephric cord to which it gives rise lie on the surface of the embryo; thus the funnel-cells are epiblastic in origin. From the nephric row one cell enlarges and enters into connection with each successive segment, as described above (fig. 5). To judge from the figures of Bergh, Wilson (**108** and **109**), and Vejdovsky, in some forms, such as Dendrobæna and Lumbricus, the funnel-cells give off the chain of posterior cells, whilst separating from the nephric row, thus remaining for some time in connection with it. In other cases, such as Criodrilus, the funnel-cells appear to separate first.[1]

In the embryo of most Oligochætes the nephridia of the first segment are developed precociously to perform the excretory functions at an early stage (fig. 25). Vejdovsky (**100** and **101**) has described these organs in Rhynchelmis, Chætogaster, Æolosoma, Nais, Allolobophora, Lumbricus, Dendrobæna, &c., and Bergh described those of Criodrilus (**9**). They consist of fine canals with an intracellular lumen, or sometimes of wider tubes; they are often ciliated, and occasionally end internally in a flame-cell; they appear to be always blind within. Externally they open either by a median dorsal pore or by two lateral pores on the first segment. In fact they closely resemble the closed pronephridia of the Platyhelminths, Entoprocta, and other groups we have already examined, or the pronephridial stage of the trunk nephridia.

The origin of the cells which form the (larval) nephridia of the first segment has not been traced; but since they arise (in some cases at least) before the division of the promesoblast cell,

[1] Bergh denies the derivation of the funnel-cell from the nephric row. Wilson rightly traced the development of the main body or canal of the nephridium from the nephric row, but failed to discover the origin of the funnel-cell itself.

Vejdovsky considers it probable that they are derived from the epiblast, a conclusion which agrees with the known development of the posterior nephridia.

The mesoblast in the Oligochætes is formed, as in all Annelids, as two germ bands, which become broken up into separate somites. The hollowing out of these gives rise to the cœlomic follicles, which increase in size, surround the gut (a stage resembling what we find in the Nemertines), and fuse below it (figs. 6 and 25). The transverse septa, between adjacent follicles, become pierced, allowing a communication from one to the other (Kowalevsky, **68**; Hatschek, **48**; Wilson, **109**; Vejdovsky, **101**). From the wall of certain of these follicles the gonads are developed, whilst others remain sterile. The number and position of the fertile follicles varies considerably according to the family of the worm in question, and even amongst different individuals of the same species (Woodward observed an earthworm with seven pairs of ovaries; **113**, **114**).

The genital ducts (peritoneal funnels) develop as a thickening of the cœlomic epithelium in the fertile segments, which grows outwards towards the epidermis, with which it fuses (figs. 6, 7, and 25). Vejdovsky, who has followed the development of these organs in several forms, such as Stylaria, Chætogaster, the Enchytrœids, and Tubificids, says: "Die Anlage des Samenleiters wiederholt sich nach dem oben Dargestellten in übereinstimmender weise bei allen bisher beoachtete Familien. Die zuerst zum Vorschein kommende Anlage des Samentrichters besteht aus einer Zellvermehrung des Peritoneums an den Dissepimenten der betreffenden Segemente" (**100**). His observations have been confirmed by Bergh (**8**) and Lehmann (**74**) in the Lumbricids.[1] In the case of the male ducts, these organs may be further complicated by the fusion of two con-

[1] Beddard (**4**) tried to show that the genital ducts were derived from the nephridia in Acanthodrilus. The few facts he brings forward from the very scanty material at his disposal do not, I think, prove his case. The theory of Claparède that the genital ducts of the Oligochætes were the modified nephridia of the genital segments was founded on an erroneous notion, since thoroughly disproved by Vejdovsky's observations.

secutive peritoneal funnels, and by the invagination of the epidermis at the genital pore to form an atrium and penis.

We may now sum up the main characteristics of the nephridia and genital ducts in this group, which has been treated at length owing to its great importance (figs. 5, 6, 7, and 25).

The nephridia of the Oligochætes are probably of epiblastic origin. They develop from large cells ("funnel-cells"), arranged metamerically outside and between each pair of somites. They pass through a more or less disguised pronephridial stage (comparable to that permanently retained in flatworms, &c.); in the first (most forms), and sometimes in the trunk segments (Chætogaster) they never develop beyond that stage. In the other segments the nephridia grow towards, and open into, the cœlom by means of a funnel formed from the original "funnel-cell."[1]

The genital ducts, on the other hand, are peritoneal funnels of undoubted mesoblastic origin, which grow outwards from the metameric genital follicles to open to the exterior. They thus have no connection with the nephridia, and differ from them entirely in their development.

Hirudinea.

So closely do the cœlom, genital ducts, and nephridia of the Leeches agree in their development with those of the Oligochætes, that their history need only be rapidly sketched.

Bürger (**16** and **19**) has carefully traced, in several forms, the origin of the whole nephridium proper (funnel and canal) from a large "funnel-cell," which comes to lie in the hinder wall of each cœlomic follicle. Just as in the previous group of worms, this cell buds off a row of cells behind which constitute the canal; the "funnel-cell" then divides up into a ring of small cells, which form the funnel of the adult nephridium (figs. 8 and 9). This organ remains closed in some forms, such as Hirudo, but opens into the cœlom in others, such as Nephelis.

[1] The branched so-called plectonephric condition of the nephridia in certain earthworms has recently been shown to arise by the secondary subdivision of originally paired nephridia (Vejdovsky, **102**; A. G. Bourne, **13**).

Meanwhile the lumen of the canal in the posterior chain of cells becomes hollowed out. The peripheral end of the canal fuses with an invagination of the epidermis, the vesicle, by means of which it opens to the exterior. The first origin of the "funnel-cells," from which the nephridia are formed, has not been traced in detail; it seems quite probable that they are derived from the nephric rows described by Whitman (**107**) in Clepsine. (They are possibly the large cells mistaken by Whitman [**106**] for the forecasts of the testes, as suggested by Bergh.)

As in the Oligochæta and Polychæta, so in the Hirudinea the nephridia of the anterior segments develop precociously in the larva. Bergh (**7**) has traced their origin as outgrowths from the epiblastic cell-rows. In Aulastoma there are four pairs, which never develop beyond the pronephridial stage, i.e. do not open internally. Bergh was also unable to find external openings (compare the nephridia of Capitella, **30** and **31**).

The cœlom develops in a normal manner as a hollowing out of the paired metameric blocks of mesoblast. Most of these cœlomic or genital follicles are fertile: an anterior pair develop the ovaries on the peritoneal wall; several posterior pairs develop the testes. That part of the cœlom which surrounds the gonads generally becomes partially separated off as a perigonadial cœlom (Bourne, **12a**; Bürger, **16**). That the genital ducts are peritoneal funnels is shown by their development, although it seems to be somewhat modified. The oviducts arise from the cœlomic epithelium surrounding the ovary, and fuse with the two ends of a forked, but median invagination of the epidermis (fig. 9) (Bürger, **19**). The vasa efferentia are similarly formed from the testes (fig. 28); they grow outwards and forwards, fusing with those in front. The most anterior join the ends of a median forked invagination of the epidermis (Nussbaum, **84**; Bürger, **19**). The complete genital ducts thus closely resemble those of some Planarians (Gunda), and differ essentially from those of the earthworm only in the number of peritoneal funnels which contribute to their formation (compare also the Vertebrates).

Archiannelida and Polychæta.

The first origin of the nephridia in these worms is not so well known as in the case of the Oligochæta. It is, however, to be remarked that in the only case where the forecast of the nephridium appears to have been traced from the beginning, it has been found to arise from the epiblast (the head-kidney in Nereis; Wilson, **110**).[1] This would agree with what we have seen occurs in most, if not all, of the groups we have already examined.

E. Meyer (**80**) has given us a most excellent description of the development of the nephridia in Polymnia and Psygmobranchus. They arise on either side from large cells, situated close to the epiblast between each pair of mesoblastic somites, with which they have no connection at this early stage. These large cells, which seem to me obviously homologous with the "funnel-cells" of the Oligochæta and Hirudinea, divide, forming a short chain of cells within which an intracellular lumen becomes hollowed out (figs. 10, 11, and 26). The mesoblastic somites become hollowed out to form the genital or cœlomic follicles, from the posterior wall of which the cœlomic epithelium becomes pushed out, forming a typical ciliated peritoneal funnel, which fuses with the internal blind end of the nephridium (figs. 11 and 26). This specialised portion of the cœlomic epithelium forms the wide-mouthed funnel of the adult nephridium (fig. 12). The lumen of the nephridial duct becomes intercellular by the multiplication of the cells which constitute its wall, and breaks through at its point of junction with the funnel on the one hand (opens, in fact, here into the cœlom), and establishes a communication with the exterior through the epidermis on the other. Such is the history of the wide-mouthed segmental organs of compound origin of the trunk. The nephridia of the first segment (or sometimes of several

[1] Hatschek (**48, 51, 54**), Salensky (**91**), and von Drasche (**27**) all consider the cells from which the nephridia are developed to be of mesoblastic origin, but the evidence on this point is not convincing. Possibly, however, as suggested for the Mollusca, they have secondarily come to be derived from the mesoblast.

anterior segments) develop in the same way as the posterior, but never pass beyond the pronephridial stage (head-kidneys); they end blindly internally with a typical flame-cell (fig. 26). Meyer figures as many as five pairs of such pronephridia in Nereis cultrifera (80)[1]. Although the head-kidneys of the Mollusca undoubtedly occasionally open internally, v. Drasche and Hatschek seem to have been mistaken in describing an internal opening in these organs in the Chætopods (see Fraipont, 40; Meyer, 80).

Fraipont appears to attribute a very similar history to the wide-mouthed trunk "nephridia" of Polygordius as Meyer has described for the trunk "nephridia" of the Tubicolous Polychætes, though his statements are less precise: "Le mésoblaste est representé de plus au niveau des muscles obliques par une masse de cellules assez confuse. C'est dans ce groupe de cellules situées au dessus des muscles obliques contre les champs musculaires longitudinaux que ce différencient les entonnoirs des organes ségmentaires et plus tard encore les organes sexuels. C'est un simple épaississement du péritoine" (40).

We see, then, that in the Polychæta nephridia are developed from large cells, which may be compared to the "funnel cells," giving rise to the nephridia in the Oligochæta. Whilst, however, in the latter the pronephridium acquires an opening into the cœlomic follicle independently of the peritoneal funnel, which acts as a genital duct; in the former, the Polychæta, the pronephridium may acquire an opening into the cœlomic follicle in the region where the peritoneal funnel is formed, fuse with it, and become an organ of double function—excretory and genital. In many cases division of labour leads to the restriction of the genital function to one set of cœlomic follicles and their funnels, and of the excretory function to another set

[1] There can now, I think, be no doubt that the head-kidneys are simply the precociously developed nephridia of the first segment; they do not open into the cœlom for the very good reason that at this stage there is, as a rule, no cœlom for them to open into. They preserve the same relations as the Platyhelminth nephridia (Hatschek, 48, 51, 54; Meyer, 80).

of cœlomic follicles and their funnels. This may lead to a corresponding differentiation of structure; in the first set the peritoneal funnel becomes the most important part, in the second the nephridial portion (such specialisation has been well described in many forms by Eisig, Meyer [80], Trautzsch [98], Cunningham [25], Marion and Bobratzky [78], &c.).

The fusion between the nephridium and peritoneal funnel does not occur in all Polychætes; fortunately, we appear still to have all the intermediate stages between this condition and that of the Oligochætes.

Meyer (80) has shown that in Nereis the nephridia of the first five segments have the typical pronephridial structure with a flame end-cell, and that in the posterior segments this end-cell (judging from his figures) opens into the cœlom (true nephrostome; compare Rhynchelmis).[1] I have also described in the Lycoridea (41) a ciliated region of the cœlomic epithelium which I believed to be the peritoneal funnel. It is, however, to Eisig that we owe the description of what appear to be intermediate stages. In Dasybranchus and Tremomastus we have conditions in which the peritoneal funnels (Genitalschlauche) are separate from the nephridia and open independently (fig. 14), and in which the two organs are connected but still open separately (fig. 13). Perhaps in certain segments of these forms and of Capitella we have the more usual Polychæte arrangement, in which the peritoneal funnel no longer acquires an independent opening (31).

Arthropoda.

It will be best to begin our review of this group with a brief recapitulation of the development of Peripatus, which has been so excellently described by Mr. Sedgwick (94), and Dr. von Kennel (64). Soon after the metameric somites have been hollowed out to form the cœlomic follicles, the upper half of each cœlomic cavity becomes nipped off from the lower half. From the wall of each of these lower cœlomic sacs a peritoneal

[1] Such would appear to be the condition in Protodrilus, where the nephridial funnels figured by Hatschek (52) are small, and provided with a flagellum.

funnel is formed as an outgrowth, which fuses with the epidermis (figs. 15 and 16). V. Kennel maintains that in Peripatus Edwardsii the mesoblastic funnel is met by an epiblastic invagination, and the question arises as to whether this invagination represents a true nephridium, in which case the segmental organ of Peripatus would be a compound organ similar to that of Psygmobranchus (see above), or whether it is merely a secondary invagination of the epidermis, such as occurs more or less pronounced in almost every case where a tube opens on to its surface (vesicle of the nephridia in the Hirudinea, peripheral end of the genital ducts of the Oligochæta, &c.). I am inclined to take the latter view, and consider the segmental organs of Peripatus as purely peritoneal funnels which have assumed the excretory functions. Whilst these organs have developed in this way, the dorsal or genital halves of the somites in the posterior segments have become fused, forming two genital tubes communicating posteriorly with the undivided cœlomic follicles of the last segment. The peritoneal funnels of this segment retain their primitive function, and develop into the genital ducts (fig. 17). The peripheral ends and median portion of the ducts are probably derived from the epidermis.

The history of the genital and excretory organs of the other groups of Arthropoda can easily be brought into agreement with the development of these parts in Peripatus. However, whereas in the latter all the cœlomic follicles give off peritoneal funnels, in the Crustacea, Arachnida, Myriapoda, and Hexapoda the peritoneal funnels are only fully developed in a very few segments. The shell glands and green glands of the Crustacea have been shown to bear the relations of peritoneal funnels (Grobben, **45**; Weldon, **104**; Marchall, **77**; Allen, **1**) and develop from the cœlomic follicles. "Bei Daphnia," says Lebedinsky (**73**), "entwickelt sich . . . die Schalendrüse als die Ausstülpung der Somatopleura, welche sich zur Max.[2] richtet und hier sich mit dem Ectoderm vereinigt." The same author describes the development of the coxal gland of Phalangium as a typical peritoneal funnel derived from a cœlomic follicle (**73**),

which description agrees with that of Laurie (**72**) of the origin of the coxal gland in Scorpio, and of Kingsley (**65**) in Limulus.

The genital cells are derived from the walls of the cœlomic follicles[1] of many segments (Heymons, **57**; Wheeler, **105**). The dorsal portion of these follicles generally fuse to form continuous tubes, or a median genital sac (as in the Crustacea). The ducts are the peritoneal funnels of one segment. The particular segment selected, so to speak, for this purpose varies much in position in different groups, and also according to sex. Wheeler, in his admirable account of the development of the Orthoptera (**105**), shows that the cœlomic follicles of all the abdominal segments at an early stage begin to develop peritoneal funnels, but that those of one segment only reach the exterior and form the genital ducts (fig. 30).

As far as we can see, therefore, there are no certain traces of true nephridia in the Arthropoda. The segmental organs, the green glands, the shell glands, and the genital ducts are all developed as peritoneal funnels.[2]

Sipunculus.

The development of the excretory organ of Sipunculus nudus has been described by Hatschek (**53**). The nephridium arises from a large cell (? "funnel-cell") which comes to lie in the wall of the cœlomic follicle. This cell divides, forming a chain of cells in which a lumen is developed. The outer end joins and opens on to the epidermis; the inner end grows towards and opens into the cœlom. The ciliated funnel is formed from the cœlomic epithelium. From this it would appear that the excretory organ of Sipunculus is of a double origin, formed by the junction of the nephridium with the peritoneal funnel, as in most Polychætes. It functions as the carrier of both genital and excretory products.

[1] Sedgwick holds that they are, in Peripatus capensis, derived from the hypoblast. If this be the case, it must be considered as due to some secondary modification.

[2] The possibility of the segmental tracheæ of the Arthropods being derived from the true nephridia should not be lost sight of. The tracheæ arise comparatively late, as a rule, as invaginations of the epidermis, and it seems not

Phoronis.

In the larva of Phoronis, Caldwell describes a pair of nephridia, slender ciliated canals blind internally (21). Their origin is still doubtful. The cœlom is developed as two pairs of follicles, of which the larger "posterior" pair is alone fertile. The excretory organs of the adult consist in Phoronis psammophila and Ph. Kowalevskii of a pair of peritoneal funnels leading to the exterior from the "posterior" cœlomic follicles (Cori, 23). According to Caldwell (22), they are developed in connection with the nephridia of the larva, and would appear to be of a compound nature like those of Polychætes. In Phoronis australis both the anterior and posterior pairs of cœlomic follicles are provided with their peritoneal funnels, which open by a common duct (Benham, 5). These funnels in Phoronis serve both as renal and genital ducts.

Ectoprocta.

No true nephridia appear to have been found in these Polyzoa. On the other hand there are two peritoneal funnels, an excellent account of which has been given by Cori in Cristatella (24). They differ from those of Phoronis only in that they open by a common median pore.

Brachiopoda.

Here the cœlomic follicles, formed as paired archenteric pouches, are provided with a pair of wide-mouthed peritoneal funnels opening to the exterior. They function as the carriers both of excretory and of genital products, and possibly the distal end of the organ represents the true nephridium (also in the Ectoprocta), which has fused with the peritoneal funnel (Morse, 83; Blochmann, 11).

impossible that they may be formed not from the nephridia, but from those late epidermal invaginations which, as we have seen, so generally occur in connection with the external opening of the peritoneal funnels. In the Arthropods above mentioned these funnels disappear in those segments which possess tracheæ.

SAGITTA.

Archenteric diverticula give rise to the three pairs of cœlomic follicles present in the adult Sagitta. The genital cells are precociously developed, and come to lie in the two posterior pairs of follicles (Hertwig, 56). Whether the genital ducts—which in the male segment, at all events, open into the cœlom by ciliated funnels—are peritoneal funnels, or are partly formed from true nephridia, cannot be decided with our present incomplete knowledge of their development.

ECHINODERMA.[1]

Only a very brief reference can be made to this highly modified group. In the larva we find a right and left cœlomic follicle, the enterocœls (derived from unpaired or paired archenteric diverticula), which may give rise to a second pair of cœlomic follicles by constriction. The anterior follicles then develop peritoneal ciliated funnels (fig. 18), which open to the exterior, fusing with paired epiblastic invaginations. As a rule only the left peritoneal funnel becomes developed (Field, 36; Bury, 20). The genital cells are developed from the wall of the posterior cœlomic follicles (MacBride, 75, 76); but how far the genital ducts can be likened to peritoneal funnels is quite uncertain.

There appears to be no trace of true nephridia.

VERTEBRATA.[1]

As is well known, the cœlom in the Vertebrates arises by the hollowing out of a series of metameric blocks of mesoblast. In the lower forms (Balanoglossus and Amphioxus) several of the anterior cœlomic follicles are formed directly as pouches from the wall of the archenteron. From these follicles, produced by either method, peritoneal funnels are developed

[1] If the treatment of these last two groups (Echinoderma and Vertebrata) seems to be somewhat too brief and dogmatic, it is that space will not allow me to discuss the subject *in extenso*. Moreover, we are here treading on such uncertain ground that I do not feel competent to treat of the structure of these animals in full detail, and offer these remarks merely as a suggestion.

which communicate with the exterior. The gonads develop from the wall of the follicles; in the lower forms a large number are fertile, but in the higher forms the genital products become restricted to a very limited region.

No true nephridia have been discovered in this group; for, until the development of the interesting segmental tubules described by Weiss (103) and Boveri (14) in Amphioxus is known, it is not possible to decide for certain on their nature.

Hemichorda or Enteropneusta.—In the anterior or proboscis region is a cœlomic cavity which appears to represent a fused pair of follicles (fig. 23), as is evidenced by the fact that it communicates with the exterior by paired peritoneal funnels (ciliated proboscis pores) in Balanoglossus Kupfferi and B. canadensis, and occasionally in Ptychodera minuta and B. Kowalevskii (Spengel, 96 and 97), and by its development as a bilobed sac in B. Kowalevskii (Bateson, 2).[1] The collar region contains a second pair of cœlomic follicles, also provided each with a peritoneal funnel or collar pore (Bateson, 2; Morgan, 82; Spengel, 97). Behind these is a third pair of follicles which do not develop funnels, but become of large size and encroach on neighbouring segments, sending back blind posterior prolongations. The posterior region contains a series of fertile cœlomic follicles, the gonads (fig. 23), each provided with a peritoneal funnel leading to the exterior.[2] Although the metamerism of this region is not very definitely pronounced, possibly having become obscured through degeneration, the genital follicles bear a remarkable resemblance, both in their structural relations and in their arrangement, to those of the Nemertines, as has already been noticed by Schimkewitsch (93 and 93a). As in the Nemertines, so also in the Enteropneusta, several genital follicles may occur in one segment.

[1] Compare the development of the corresponding anterior pair of cavities in Amphioxus (Hatschek, 49).

[2] If this explanation be correct, the gill-slits of Balanoglossus are metameric and intersegmental as in other Vertebrates. If not correct, we have an almost incredible state of things in which the genital cells are shed into a cavity which is not the cœlom.

Craniata.—Owing mainly to the recent researches of van Wijhe (99), Rückert (89 and 90), Semon (95), and others, it is now generally concluded that the Craniates originally possessed a metameric series of pronephric tubules, or peritoneal funnels, opening independently to the exterior. In existing forms the funnels, which grow out from the cœlomic follicles, sometimes reach the epiblast as solid rods (fig. 19); they then fuse with each other to a common duct which opens into the cloaca (fig. 31), constituting what is known as the pronephros and its pronephric duct. In his excellent paper on the development of the renal system of Ichthyophis, speaking with regard to E. Meyer's theory, Semon says: "Die segmentalen Ausführgänge der segmentalen Genitalfollikel oder Ursegmente übernehmen neben ihrer ursprünglichen auch noch exkretorische Funktion, sie werden zu Vornierkanälchen" (95).

To conclude our general survey it may be said: that the cœlom can be traced from its smallest beginning as a cavity or cavities in which are developed the gonad-cells: it grows gradually in size and importance until it becomes the body cavity in which the viscera rest; that the genital ducts (with a few possible exceptions due to secondary modifications) are homologous throughout the Cœlomata; that the nephridia, which have often been confused with these ducts, can always, when they occur, be distinguished from them; and finally, that the cœlom may secondarily acquire a renal function, in consequence of which the peritoneal funnels supersede the nephridia proper as excretory ducts.

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EXPLANATION OF PLATES 44 & 45,

Illustrating Mr. Edwin S. Goodrich's paper on "The Cœlom, Genital Ducts, and Nephridia."

Reference Letters.

c. Cœlomic or genital follicle. *ep. i.* Epidermal invagination. *neph.* True nephridium. *p.f.* Peritoneal funnel developed from the cœlomic epithelium.

In all the diagrams the outline of the cœlom, the peritoneal funnels, and the genital cells, are drawn in red. The epiblast and hypoblast are darkly shaded. The mesoblast is lightly shaded. The true nephridia are drawn in black.

Fig. 1.—Diagrammatic plan of the cœlom, genital ducts, and nephridia in the Planaria.

Fig. 2.—Similar plan of a young Nemertine.

Fig. 3.—Plan of a mature Nemertine.

Fig. 4.—Plan of the cœlom, &c., in the Entoprocta.

Fig. 5.—Plan of the cœlom and nephridium in an embryo Oligochæte.

Fig. 6.—Later stage of the same, showing the nephridia in the pronephridial condition.

Fig. 7.—Plan of the cœlom, &c., in an adult Oligochæte (Lumbricus).

Fig. 8.—Plan of the cœlom and nephridia in an embryo leech.

Fig. 9.—Plan of the cœlom, &c., in the Hirudinea.

Fig. 10.—Plan of the cœlom and nephridia in an embryo Polychæte.

Fig. 11.—Later stage of the same, showing the pronephridium about to fuse with the peritoneal funnel.

Fig. 12.—Plan of the cœlom, &c., in the Polychæta possessing wide-mouthed "compound nephridia," the nephridium having fused with the peritoneal funnel.

Fig. 13.—Plan of the cœlom, &c., in certain segments of Tremomastus and Dasybranchus in which the nephridial funnel is continuous with the genital or peritoneal funnel.

Fig. 14.—Plan of the cœlom, &c., in certain segments of Dasybranchus caducus, in which the nephridial funnels are independent of the peritoneal funnels.

Fig. 15.—Plan of the cœlom and developing peritoneal funnels in an embryo Peripatus.

Fig. 16.—Plan of the cœlom and peritoneal funnels in a trunk segment of Peripatus. The cœlomic follicles on either side have become separated into a ventral and a dorsal portion, forming the genital tube.

Fig. 17.—Plan of the cœlom and peritoneal funnels in the posterior segment of Peripatus.

Fig. 18.—Plan of the cœlomic follicles (enterocœls) and developing peritoneal funnels in an embryo Echinoderm (Asterias).

Fig. 19.—Plan of a stage in the development of the cœlom and peritoneal funnels (pronephric tubules) of an Elasmobranch.

Fig. 20.—Plan of the cœlom and nephridia (pronephridial stage) in an embryo Mollusc.

Fig. 21.—Plan of the cœlom and developing peritoneal funnels (excretory organs of the adult) of a Mollusc.

Fig. 22.—Farther stage of the same, after the peritoneal funnel has fused with the epidermal invagination.

Fig. 23.—Plan of a longitudinal section of Balanoglossus, showing the cœlomic follicles and peritoneal funnels.

Fig. 24.—Plan of a longitudinal section of a Nemertine, showing the cœlomic follicles and peritoneal funnels before the latter have reached the epidermis (the nephridia are represented in the same region as the genital follicles).

Fig. 25.—Plan of a longitudinal section of the nephridia, cœlom, and developing peritoneal funnels in a larval Oligochæte.

Fig. 26.—Similar plan of a larval Polychæte.

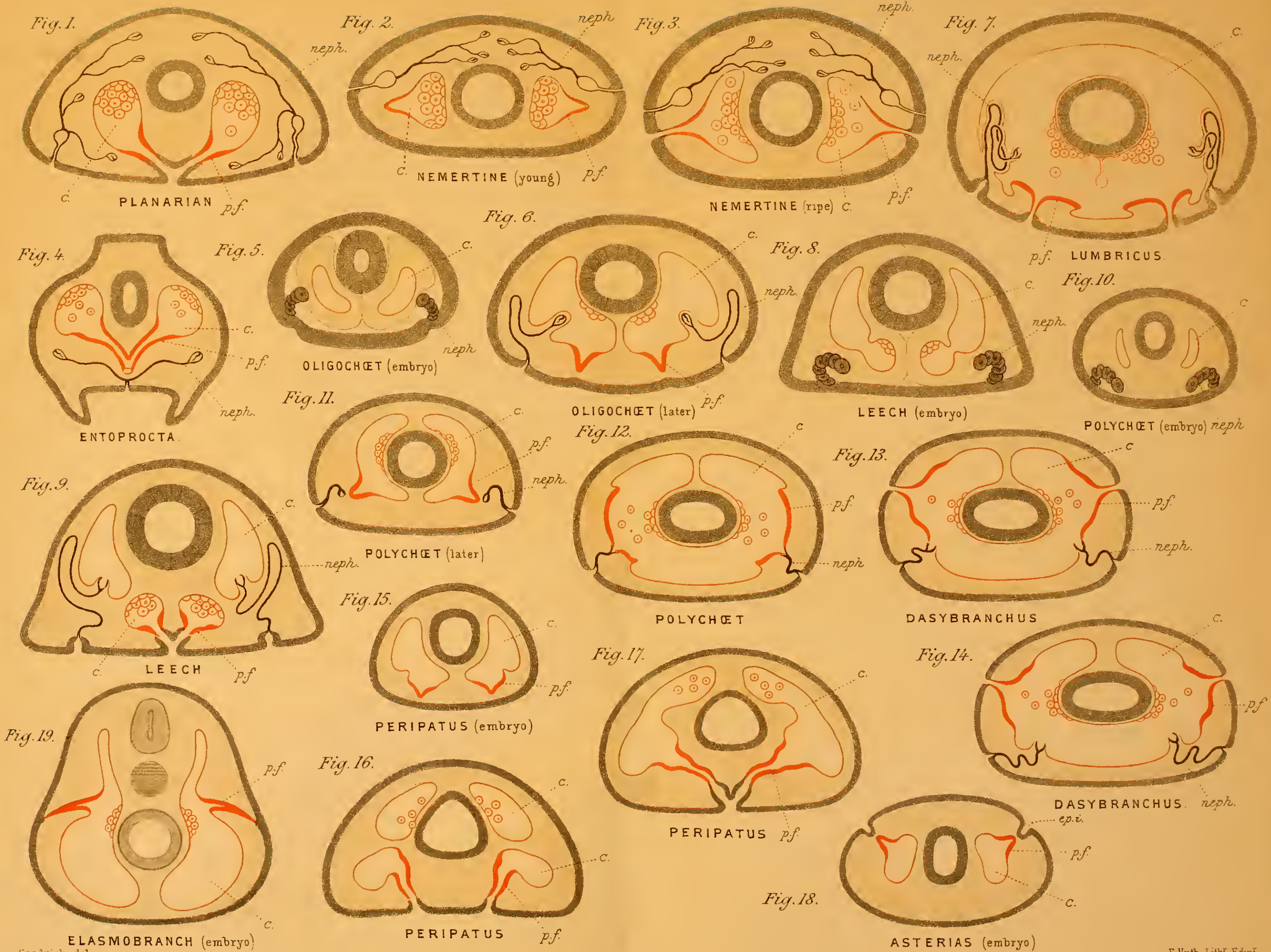
Fig. 27.—Plan of a longitudinal section of the cœlom and peritoneal funnels in an embryo Vertebrate.

Fig. 28.—Plan of a longitudinal section of the cœlom, peritoneal funnels, and nephridia of a Leech.

Fig. 29.—Plan of a longitudinal section of the cœlom, &c., of an Oligochæte.

Fig. 30.—Plan of a longitudinal section of the cœlom and developing peritoneal funnels of an embryo Insect.

Fig. 31.—Plan of cœlom and peritoneal funnels (pronephric tubules) of a Vertebrate.



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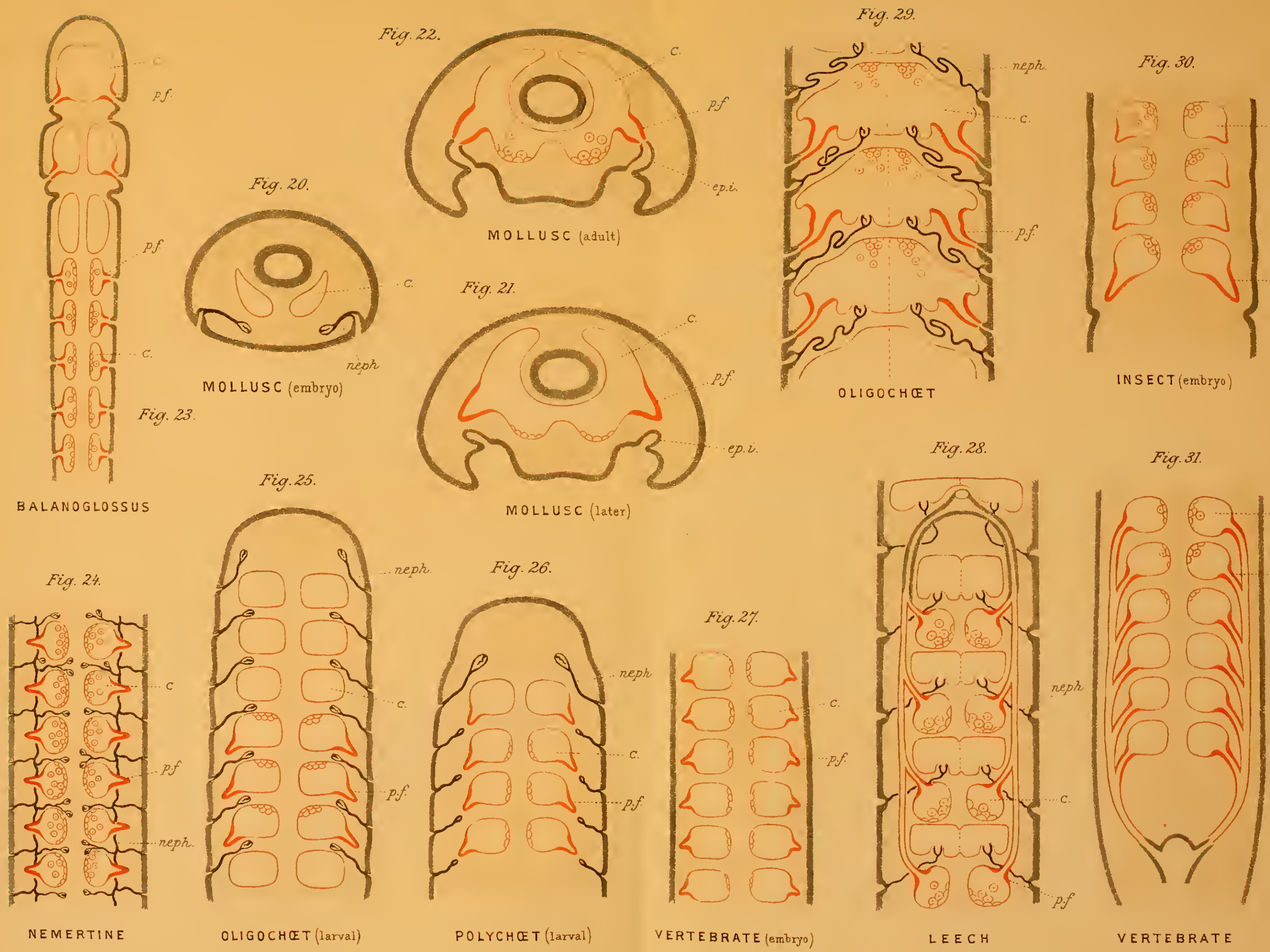

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